Comparative microclimatology and plant responses in *Encelia* species from contrasting habitats

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The microclimate, water relations, and leaf temperatures of two closely related arid land shrubs of the genus *Encelia* (Asteraceae) in south-western North America are compared. The two species differ primarily in leaf pubescence; *Encelia californica* from cool, relatively wet coastal sites has essentially glabrous leaves, whereas *Encelia farinosa* from relatively hot, dry inland sites has heavily pubescent leaves. The two habitats contrasted sharply in air temperature, atmospheric vapor pressure deficit, and precipitation. When leaf water potentials were compared, they were lower for *Encelia farinosa*, the species which occurs on sites with less precipitation. Leaf conductances to water vapor were similar in both species at similar times of the year. Leaf temperatures of *Encelia californica* were greater than air temperature, whereas leaf temperatures of *Encelia farinosa* were normally less than air temperature because of differences in leaf spectral characteristics caused by pubescence and because relative humidities were lower at the inland sites. The significance of leaf pubescence in adapting to the more arid desert environment is discussed.

Introduction

The desert environments of south-western North America are characterized by high levels of incoming solar radiation, high summer air temperatures, and limited soil moisture availability (MacDougal, 1908; Shreve & Wiggins, 1964; Sellers & Hill, 1974). These environmental factors have selected for the evolution of a diversity of morphological and physiological adaptations in plants to cope with the harsh conditions (MacDougal, 1908; Shields, 1950; Shreve & Wiggins, 1964; Ehleringer, 1984a). One such leaf adaptation is the presence of a reflective leaf pubescence. It is often observed that leaves of a given species become more reflective along gradients of increasing aridity, or that there is a species replacement such that species in more arid habitats have more pubescent leaves (Ehleringer, 1984b).

Encelia farinosa is one of the most common drought-deciduous leaved species in the Sonoran Desert that is capable of producing more pubescent leaves in response to changes in environmental conditions (Shreve, 1924; Walter, 1931; Cunningham & Strain, 1969; Ehleringer & Björkman, 1978a; Ehleringer, 1982). During the onset of drought periods, *E. farinosa* responds to the changes in environmental conditions by producing new leaf types with increased pubescence.

Previous studies have shown that leaf spectral characteristics in *E. farinosa* were greatly affected by the extent of pubescence development (Ehleringer, Björkman *et al.*, 1976; Ehleringer & Björkman, 1978a; Ehleringer, 1982). Leaf absorptance to photosynthetically useful solar radiation (400–700 nm) was reduced from 81 to 29 per

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cent when lightly and heavily pubescent leaves were compared. The equivalent decrease in total solar radiation absorptance (400–3000 nm) is from 48–9 per cent. The change in leaf spectral characteristics had the net effect of decreasing leaf temperature by 5–10 °C and decreasing transpiration rate by a third (Ehleringer & Mooney, 1978). The adaptive value of the pubescence resulted primarily from its effects on reduced leaf temperature and decreased water loss. Additionally, the amount of leaf pubescence varied with temperature and drought during the growing season in such a way that net carbon gain was maximized (Ehleringer & Mooney, 1978; Ehleringer, 1980).

For this study, two species representing opposite ends of an aridity gradient and extremes in leaf pubescence were chosen; these were *Encelia farinosa* and *Encelia californica*. Leaves of both species are similar except for the degree of pubescence. *E. farinosa* is found in hot, dry habitats and occurs throughout most of the Sonoran Desert, extending into portions of the Mojave Desert (Munz, 1959; Shreve & Wiggins, 1964) (Fig. 1). This species is characterized by heavily pubescent whitish leaves, with the leaf hairs occurring on both the upper and lower surfaces. Leaves of *E. californica*, on the other hand, have very lightly appressed pubescence, and are distinctly green in color. *E. californica* is restricted to the cooler, more mesic habitats along the coasts of southern California and upper Baja California (Munz, 1959; Shreve & Wiggins, 1964) (Fig. 1). The purpose of this study was to compare the leaf water relations and microclimatology of these two species growing in the vastly different habitats.
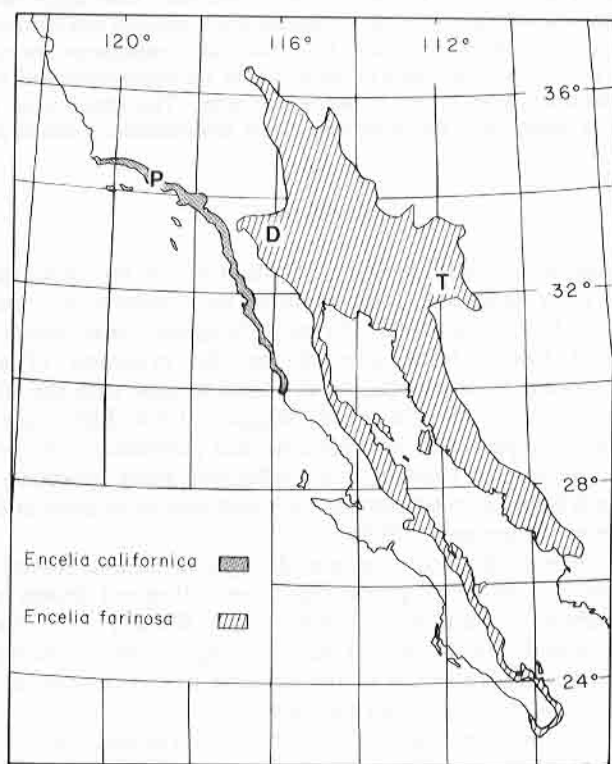

Figure 1. Distributions of *Encelia californica* and *Encelia farinosa* in south-western North America. Based on information in Shreve and Wiggins (1964) and personal observations. Locations: D, Deep Canyon; P, Point Mugu; T, Tucson.

Materials and methods

Field study sites

Field studies of *E. farinosa* were concentrated at two sites: the Boyd Desert Research Center in Deep Canyon, California (33°41'N; 116°24'W), and Tumamoc Hill in Tucson, Arizona. The Deep Canyon Laboratory is in the Colorado Desert at an elevation of approximately 300 m. The vegetation is typical of the Colorado Desert, being dominated primarily by perennial species such as *Acacia greggii, Ambrosia dumosa, Cercidium floridum, Encelia farinosa, Hyptis emoryii, Larea divaricata, Opuntia basilaris, Opuntia bigelovii*, and *Prospis glandulosa*. Precipitation occurs chiefly during the winter months and averages 109 mm annually (U.S. Weather Bureau records) (Fig. 2). The mean maximum daily air temperature is 38·3 °C for July, but drops to 17·8 °C for the mean maximum during December and January.
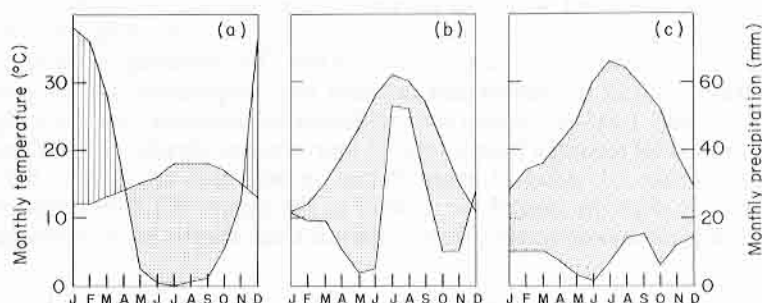

Figure 2. Climate diagrams for Point Mugu, California, Tucson, Arizona, and Deep Canyon, California. *Encelia californica* occurs at Point Mugu, while *Encelia farinosa* is common in Tucson and Deep Canyon. The left-hand axis is mean monthly temperature and the right-hand axis is mean monthly precipitation (based on 10+ years records). The dotted area represents a period when the temperature line exceeds precipitation and the vertical hatched area vice versa. (a) Point Mugu, mean annual temperature 15·2 °C, mean annual precipitation 357 mm; (b) Tucson, 20·2 °C, 271 mm; (c) Deep Canyon, 23·2 °C, 109 mm.

The Tumamoc Hill study site is located at the edge of the city of Tucson, Arizona, at an elevation of approximately 750 m (32°15'N; 110°57'W). The study area is the site of the old Carnegie Institution of Washington Desert Laboratory. The vegetation of the area is characteristic of the Arizona Upland in the Sonoran Desert (Shreve & Wiggins, 1964). The dominant perennial species include *Acacia greggii, Carnegia gigantea, Cercidium microphyllum, Encelia farinosa, Ferocactus wislizenii, Larrea divaricata*, and *Prosopis juliflora*. Rainfall patterns on Tumamoc Hill are distinctly bimodal; there are definite winter and summer rainy periods. The total annual precipitation 271 mm of which approximately 50 per cent falls in each of the rainy seasons (Fig. 2). Mean daily maximum air temperatures are 38·8 °C for July and 18·9 °C for January (U.S. Weather Bureau records).

Encelia californica was studied at Point Mugu, California (34°5'N; 119°3'W). This moderately cool, coastal site in southern California is at sea level and is an area dominated by the coastal sage community. The dominant species include *Artemisia californica, Encelia californica, Rhus integrifolia*, and *Salvia mellifera*. Precipitation falls almost exclusively during the winter months and averages 357 mm annually (Fig. 2). Mean maximum air temperatures vary from 23·4 °C in July to 18·4 °C in January (U.S. Weather Bureau records).

Microclimatic measurements

The micrometeorological variables measured were total net radiation, total and diffuse solar radiation, wet-bulb, dry-bulb, leaf and soil temperatures, and wind speed. Net radiation was measured with a net radiometer (Micromet Instruments, Bothell, Washington, U.S.A.) and solar radiation with a pyranometer (model LI-200S, Lambda Instruments, Lincoln, Nebraska, U.S.A.). The photon flux between 400 and 700 nm was also measured. These readings will not be presented, however, as they were equal at all times to a constant fraction of the total solar radiation values.

Leaf and air temperatures were measured with 36 gauge copper–constantan thermocouples (0·25 mm diameter). The wet bulb temperature was measured with a thermocouple in the shape of a ring. A very thin film of water covered this ring, causing the thermocouple to approach the wet bulb temperature when exposed to the air. This technique for measuring the wet bulb temperature appeared to be independent of wind speed across the thermocouple (Caldwell & Caldwell, 1970). Leaf–air temperature differentials were measured with two copper–constantan thermocouples in series and 1 cm apart, with one thermocouple inserted into the lower leaf surface and the second thermocouple in the shaded air directly below the leaf. The resulting signal represented a precise determination of the differences between leaf temperature and air temperature adjacent to the leaf. Leaf–air temperature differentials reported here each represent a mean of 16 individual readings from a total of four separate shrubs. Vertical bars on the plotted data indicate ±1 standard error. When vertical bars are absent, the standard error was smaller than the size of the symbol in the figure. All field temperature and micrometeorological measurements were collected from shrubs on south-facing slopes.

Plant water relations

Leaf conductances to water vapor were measured on attached leaves using a transit time porometer (Kanemasu, Thurtell *et al.*, 1969). The leaf conductance values presented represent the means of readings from four separate leaves. Leaf water potentials were measured using a pressure chamber (Scholander, Hammel *et al.*, 1965) and the data presented are the means of two or three leaves. Vertical bars on the leaf conductance and leaf water potential indicate ±1 standard error. When vertical bars are absent, the standard error was smaller than the size of the symbol in the figure. Mature outside canopy leaves on the south side of the shrub were used for all analyses.

Leaf spectral characteristics

The leaf absorptance of solar radiation in the 400–700 nm waveband was measured in the field using an Ulbricht integrating sphere coupled to a heliostat (Ehleringer, 1981). Calculations of the leaf absorptance to the entire solar spectrum (400–3000 nm) were based on regression equations relying on the 400–700 nm leaf absorptance (Ehleringer, 1981). The leaf absorptance data presented are the means of five mature leaves.

Leaf activity

Estimates of leaf activity on shrubs at each site was determined by counting the number of mature, live leaves on individual stems. The leaf activity data are presented as the means of 10 stems on 10 different shrubs. Vertical bars on the plotted data indicate ±1 standard error. At Deep Canyon, measurements were also collected on five shrubs which received 20 litres per week supplementary watering throughout the entire measurement period.

Results

Leaf activity

Water appeared to be the chief factor influencing vegetative activity in both *E. californica* and *E. farinosa*. Vegetative activity, as measured using the number of leaves per twig, varied throughout the year with precipitation (Fig. 3). The pattern was much clearer for *E. californica* at Point Mugu where precipitation fell almost exclusively during the winter and spring as is typical of Mediterranean-type climates. *E. farinosa* was potentially active at any time of the year following major precipitation events. While vegetative activity is typically limited to the bimodal precipitation periods (Fig. 2), it is clear from Fig. 3 that leaves of *E. farinosa* could persist throughout the late spring and fall periods. Moreover, at Deep Canyon, where some plants received supplementary watering, vegetative growth continued throughout the year. During the driest periods, one or two leaves persisted on *E. farinosa* twigs, whereas *E. californica* twigs were completely leafless during the drought periods (Fig. 3).
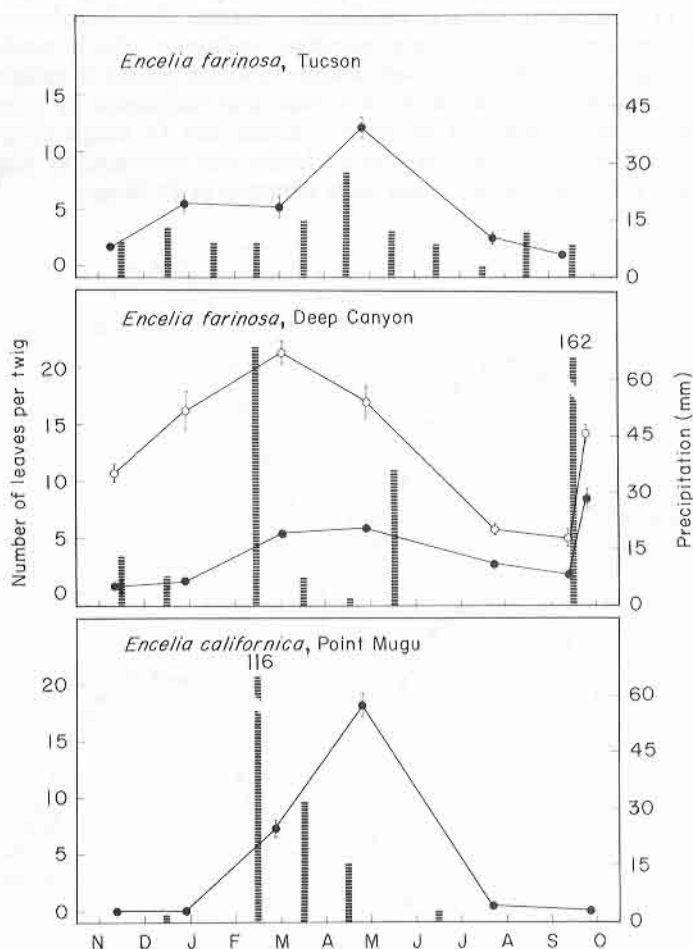

Figure 3. Seasonal leaf activity patterns for *Encelia californica* and *Encelia farinosa* shrubs in Tucson, Deep Canyon, and Point Mugu (○—○, watered; ●—●, unwatered). Vertical line indicates ± standard error. Also presented are monthly precipitation totals for these three sites (vertical hatched bars). Data are for the period November 1975 through to September 1976.

Microclimate

Microclimate variables were measured on *E. farinosa* shrubs on Tumamoc Hill on a clear day in each of the four seasons. Sampling dates for the winter, spring, summer, and fall seasons were 26 December, 27 April, 24 July, and 9 November, respectively. Comparisons between sites is appropriate, since measurements on different sites were collected on adjacent days with the plants exposed to similar 'weather' conditions.

On clear days total solar radiation varied sinusoidally through the day, with net radiation over an *E. farinosa* shrub being roughly two-thirds of the total solar radiation (Fig. 4). Midday total solar radiation ranged from a maximum of 930 W/m^2 in the spring to a minimum of 580 W/m^2 in the winter.

The microclimate of *E. californica* shrubs was measured on a winter day (29 February) and a spring day (26 April) since these were the only two seasons when leaves were present. 29 February was a partly cloudy day, typical of this time of year, and total solar radiation values did not exceed 620 W/m^2 (Fig. 5). In contrast, 26 April was clear and total solar radiation intensities rose to 920 W/m^2 at midday.

From the climate diagrams of Fig. 2, it appeared that the *E. farinosa* habitats are not only drier (less precipitation), but also significantly warmer than *E. californica* habitats, which may be because of the strong maritime influence which tends to buffer temperature change, and/or the increased cloudiness which results in reduced radiative heating in coastal sites. On clear days there was little difference in either the solar radiation or net all-wave radiation values at Tucson and Pt Mugu (Figs 4 and 5). However, the frequency of cloudy days at Pt Mugu was substantially higher than at Tucson and early morning coastal clouds were common at Pt Mugu.
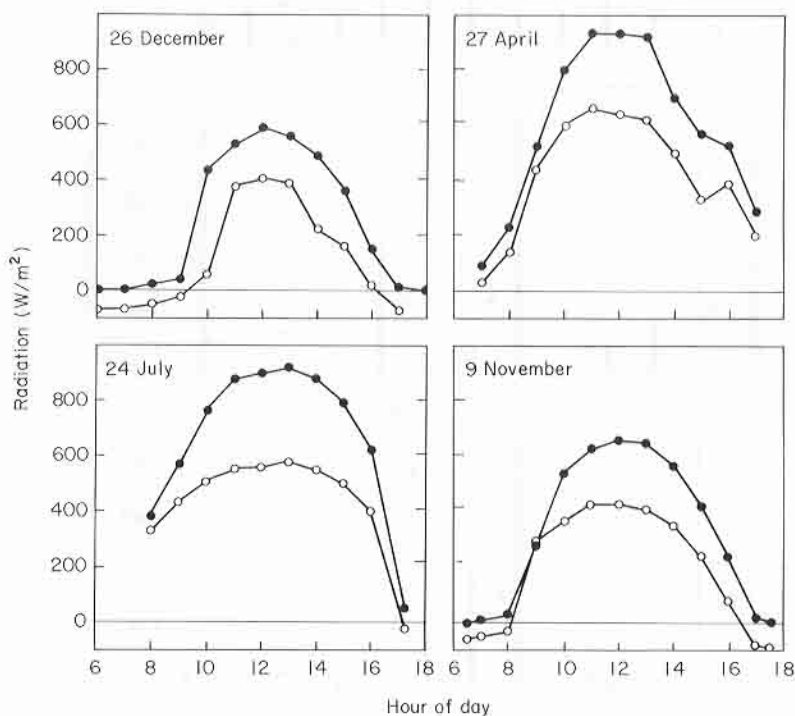

Figure 4. Diurnal courses of total solar radiation and net all-wave radiation over *Encelia farinosa* shrubs in Tucson, Arizona for four dates representing different seasons of the year. Dates are 26 December 1975, 27 April 1976, 24 July 1976, and 9 November 1975. ●—●, Total solar; ○—○, net.
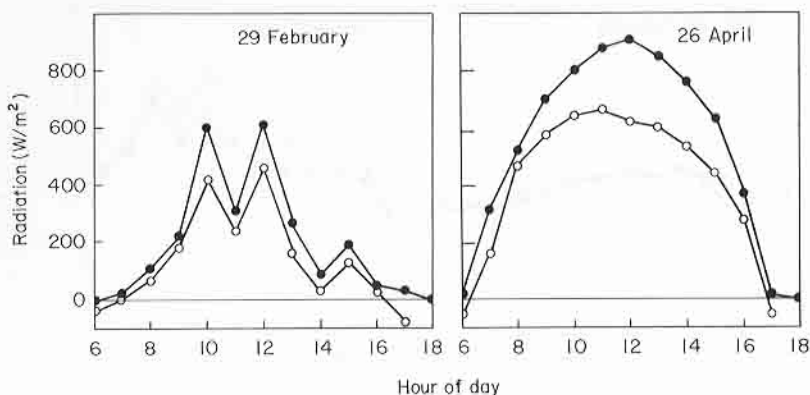
Figure 5. Diurnal courses of total solar radiation and net all-wave radiation over *Encelia californica* shrubs at Point Mugu, California, for two dates representing the two seasons of the year when these plants have leaves. Dates are 29 February 1976 and 26 April 1976. ●—●, total solar; ○—○, net.

Air temperatures at leaf height were substantially cooler at Pt Mugu than at Tucson, except during the winter (Figs 6 and 7). In winter (26 December and 29 February) daytime air temperatures varied between 12·3 and 17·4 °C and between 3·2 and 17·8 °C at Pt Mugu and Tucson, respectively. These values were representative of temperatures for these times of the year. At this same time, leaf temperatures of both species were equal to or slightly higher than air temperature, a point that will be discussed further later.

By spring (26–27 April) air temperatures at both sites had increased, but the Pt Mugu site was still appreciably cooler than Tucson (Figs 6 and 7). Midday air temperatures
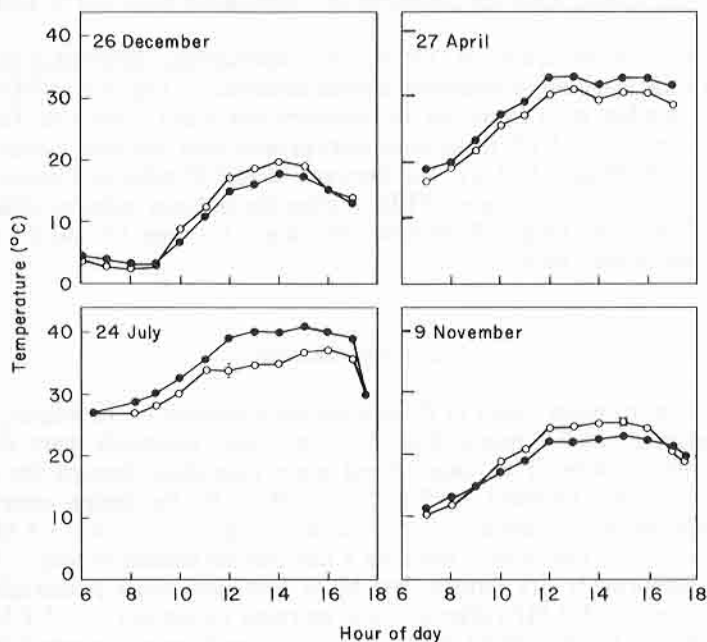

Figure 6. Diurnal courses for leaf and air temperatures at plant height for *Encelia farinosa* shrubs in Tucson, Arizona. Measurements were collected at the same time as those in Fig. 4. Vertical line indicates ± standard error. ●—●, air; ○—○, leaf.
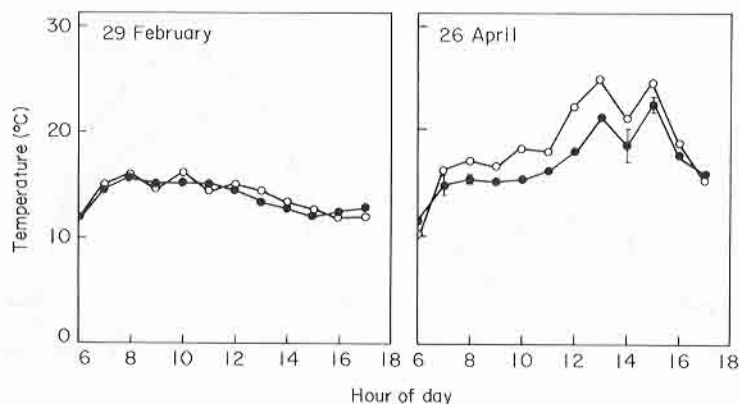
Figure 7. Diurnal courses of leaf and air temperatures at plant height for *Encelia californica* shrubs at Point Mugu, California. Measurements were collected at the same time as those in Fig. 5. Vertical lines indicates ± standard error. ●—●, air; ○—○, leaf.

were in the mid 20 °C at Pt Mugu, and in the mid 30 °C at Tucson. However, the differences in leaf temperature between the sites were not as extreme since *E. californica* leaf temperatures (17·3–25·0 °C) were warmer than air temperature and *E. farinosa* leaf temperatures (21·6–29·6 °C) cooler than air temperature.

In the summer and fall, *E. californica* was dormant and measurements were only collected at the Tucson site. In the summer air temperatures above 40 °C as experienced on 24 July (Fig. 6) were common. Leaf temperatures were always substantially cooler (5 °C or more) than air temperature. Air temperatures on 9 November (Fig. 6) were typical for the fall season. Leaf temperatures on 9 November were 1–2 °C higher than air temperature.

The water vapor pressure deficits (VPDs) were substantially different at the two sites, consistent with the maritime–continental habitat differences. Day-time VPDs fluctuated between 2 and 4 mbar at Pt Mugu on 29 February and 3 and 8 mbar in Tucson on 26 December. By spring, the VPD differences were greater with day-time values of between 8 and 15 mbar at Pt Mugu (26 April) and between 16 and 37 mbar at Tucson (27 April). Plants at Tucson experienced higher VPDs during the summer months with maximum VPDs in the 35–60 mbar range. Wind velocities ranged between 1·5 and 2·5 m/s at both sites on all measurement days.

Leaf water relations

Leaf conductances to water vapor in *E. farinosa* were greatest in the winter, when they reached a maximum of 9.7 mm/s (Fig. 8). Leaf water potentials were also greatest during the winter months. The range of leaf water potentials through the day on the winter sample date was between −0·9 and −2·0 MPa. By the spring sample date (27 April), leaf water potentials had decreased to a daily range of −2·2 to −3·4 MPa. Spring leaf conductances were also lower, reaching a daytime maximum of only 2·7 mm/s.

During the abnormally dry sample date of 24 July, leaf water potentials reached a midday minimum of −3·3 MPa after an early morning maximum of −2·2 MPa. These values were similar to the spring values. Similar trends were observed for the leaf conductance measurements. Leaf conductances were greatest (3·4 mm/s) at 0800 hours, and then fell to a midday minimum of 1·1 mm/s before again rising to 1·7 mm/s in the late afternoon.
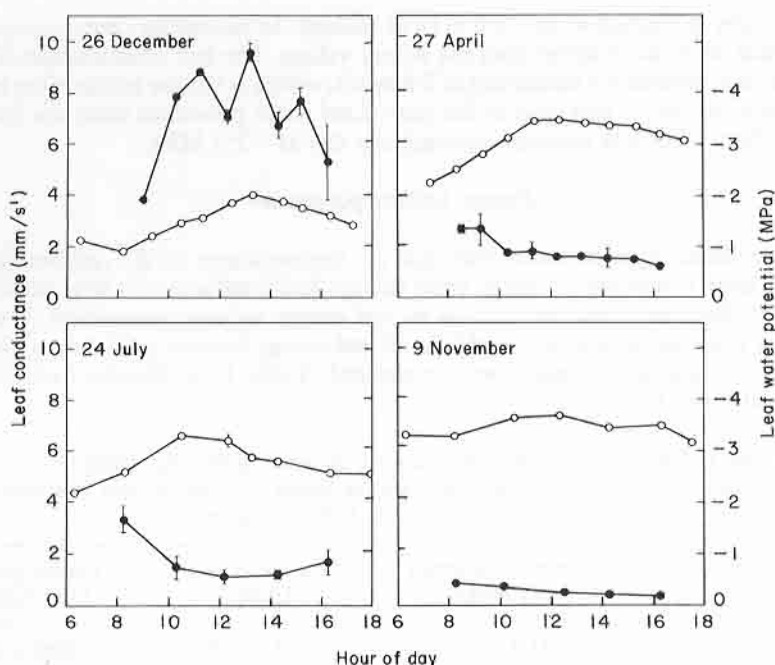
Figure 8. Diurnal courses of leaf conductances to water vapor and leaf water potentials for *Encelia farinosa* in Tucson, Arizona. Measurements were collected at the same time as those in Fig. 4. Vertical line indicates ± standard error. ●—●, conductance; ○—○, water potential.

The *E. farinosa* shrubs showed little activity during the fall sample period. Leaf water potentials were very low, ranging from −3·2 to −3·5 MPa during the day. Leaf conductances did not rise above 0·9 mm/s.

The leaf conductances to water vapor in *E. californica* were greatest on the winter sample date when they reached 11·6 mm/s, although midday values were generally in the range of 9–11 mm/s (Fig. 9). Leaf water potentials were also significantly greater at this time of the year. Leaf water potentials on 29 February did not fall below − 0·7 MPa. For approximately the same period of the year (26 December), the leaf water potentials of *E*.
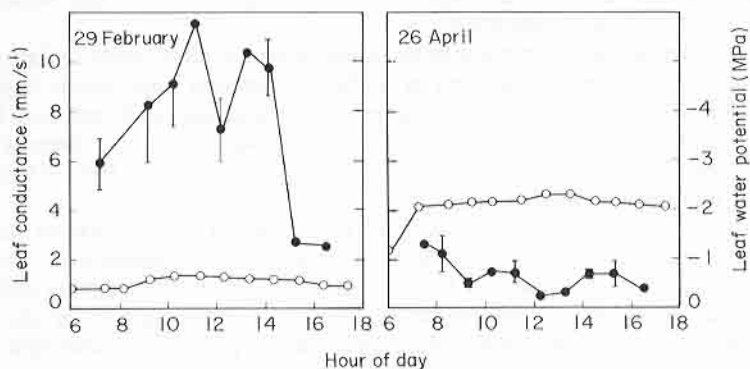

Figure 9. Diurnal courses of leaf conductances to water vapor and leaf water potentials for *Encelia californica* at Point Mugu, California. Measurements were collected at the same time as those in Fig. 5. Vertical line indicates ± standard error. ●—●, conductance; ○—○, water potential.

farinosa shrubs in Tucson were -2.0 MPa at midday. In the spring, leaf conductances in *E. californica* were much lower than the winter values. The leaf conductances fluctuated during the day, attaining a maximum of 2.6 mm/s, which is similar to the value measured in *E. farinosa* leaves for this time of the year. Leaf water potentials were also lower than in winter, but essentially constant through the day at -2.3 MPa.

Energy balance parameters

There were differences between leaf and air temperatures of *E. californica* and *E. farinosa* in their respective habitats, even though leaf conductances were similar. This implies that there were also differences in leaf energy balance parameters. During the 1976 spring growing period, three additional leaf energy balance parameters (leaf angle, leaf width, and leaf absorptance) were measured (Table 1) on *Encelia* from Pt Mugu, Tucson, and Deep Canyon.

Table 1. *Leaf energy balance characteristics of leaves of* Encelia californica *and* Encelia farinosa. *The data presented are the means ± standard error and were collected early in the spring 1976 growing season*

	Encelia californica (Pt Mugu)	Encelia farinosa (Tucson)	Encelia farinosa (Deep Canyon)
Leaf angle (degrees)	41.8 ± 3.5	26.3 ± 2.9	26.0 ± 3.0
Leaf width (mm)	16.2 ± 0.5	13.3 ± 0.5	10.7 ± 0.4
Leaf absorptance (400–700 nm) (%)	81 ± 0.3	60 ± 3	54 ± 2
Leaf absorptance (400–3000 nm) (%)	47	32	28

Leaf angles differed significantly between *E. californica* and *E. farinosa* (Table 1). The steeper leaf angle in *E. californica* resulted in a relatively higher incident solar radiation load during the winter than would be incident on *E. farinosa* leaves. However, during the late spring and early summer when the sun is higher in the sky, *E. californica* leaves will have a 20 per cent lower incident solar radiation load by virtue of the steeper leaf angle.

Leaf widths were significantly different between *E. californica* and *E. farinosa* (Table 1), although these differences were not large. The leaf width differences would not have a pronounced effect on heat exchange (less than 10 per cent on leaf boundary layer conductance), or on leaf temperature.

There were substantial differences in leaf absorptance of short-wave radiation between *E. californica* and *E. farinosa*, as well as within *E. farinosa* populations depending on location (Table 1). The absence of leaf pubescence would lead to 47 per cent increase in short-wave interception by *E. californica* leaves compared to *E. farinosa* leaves in Tucson. When the comparison is made with *E. farinosa* leaves from Deep Canyon, interception increases by 68 per cent.

Direct comparisons of leaf temperatures of *E. californica* and *E. farinosa* plants under natural conditions clearly showed that leaf temperatures were higher in *E. farinosa* than in *E. californica*. In part, these leaf temperature differences were due to differences in environmental variables (air temperature, long-wave irradiance from the sky, and absolute humidity) and in part due to differences in leaf parameters (absorptance, angle, and leaf conductance). While direct comparisons were not possible, it was possible to estimate the impact of various leaf parameters on leaf temperature through an energy budget analysis (Miller, 1972). Using data from Table 1, midday spring irradiances, 30 °C air temperature, 2 m/s wind velocity, and assuming a constant leaf conductance, the energy budget analyses showed that the leaf absorptance was the most important

factor influencing leaf temperature. At 10 per cent relative humidity and 26° leaf angle, the calculated leaf temperature was 29·6 °C for a leaf absorptance of 0·57 (400–700 nm) and 31·0 °C for a leaf absorptance of 0·85. With relative humidity increased to 60 per cent, the calculated leaf temperatures were 30·2 °C and 31·6 °C, respectively. Increasing leaf angles to 42° decreased leaf temperatures by only 0·4 °C in both sets of relative humidity and absorptance conditions. Thus, we conclude that changes in leaf absorptance were the most significant leaf parameter affecting tissue temperatures. These calculations underestimate the magnitude of the leaf–air temperature differences observed between the two sites. It is likely that the long-wave radiation from the sky was higher at Pt Mugu (the more humid site) and that this increased heat load contributed to the higher leaf temperatures observed at this site. A lack of sufficient long-wave radiation estimates at the two sites prevents a precise estimate of how important the long-wave radiation differences might be in influencing leaf temperature.

Discussion

Leaf pubescence has been regarded historically as an adaptation to arid habitats (Schimper, 1903; Warming, 1909; Coulter *et al.*, 1911), but few data are available to compare the performances of pubescent and non-pubescent leaved species. This study has concentrated on a comparison of the microclimate of plants with heavily pubescent and essentially non-pubescent leaves, and on the physiological responses of these leaves along an aridity gradient at times of the year when plants are active. The system chosen for study was *Encelia*, a genus of approximately a dozen taxonomically recognized species with adjoining but sympatric distributions in the arid regions of south-western North America and western South America (Blake, 1913; Shreve & Wiggins, 1964; Ehleringer, Mooney *et al.*, 1981). Members of the genus are relatively short lived suffrutescent shrubs with drought-deciduous leaves. The species are quite similar morphologically, except for differences in leaf pubescence, leaf size, and the disk flower color. The comparison for this study was between two species occupying the extremes of the aridity gradient.

From the climatic data, it is clear that both the macroclimate and microclimate of *E. farinosa* habitats are more harsh than in *E. californica* habitats. Air temperatures and VPDs are greater and more variable, and precipitation is much less. Given these extremes in climate, large differences in the physiological responses of leaves of *E. californica* and *E. farinosa* may be anticipated. While it appears that leaf water potentials are different and consistent with habitat aridity, the air–leaf temperature differentials and leaf conductances to water vapor are inconsistent. The leaf temperatures of the two species are rather similar to each other even though air temperatures varied significantly. This appears to be due mainly to the decreased short-wave radiation absorption by the leaf surface, associated with the *E. farinosa* leaf pubescence, resulting in a reduced leaf temperature (Ehleringer & Mooney, 1978).

The adaptive value of leaf pubescence in *E. farinosa* is through its effects on both water loss and carbon gain. Increased leaf temperatures have been shown to reduce net photosynthesis and increase water loss in *E. farinosa* (Ehleringer & Björkman, 1978*b*). As seasonal air temperatures and drought increase during the season, leaf pubescence in *E. farinosa* varies such that net carbon gain is maximized (Ehleringer & Mooney, 1978; Ehleringer, 1980).

The leaf pubescence which results in an increased reflectance (decreased absorptance) is apparently a 'blanket' reflector, at least over the visible wavelengths (Ehleringer & Björkman, 1978*a*). When the hairs of *E. farinosa* are removed, the absorptance spectrum is nearly identical to that of *E. californica*. This suggests that the leaves of all *Encelia* species along aridity gradients (both temperature and precipitation) have the same basic absorptance, but are covered with variable amounts of hair giving the characteristics of a blanket reflector. Given that Ehleringer & Björkman (1978*b*) have shown that basic

photosynthetic characteristics are nearly identical in *E. californica* and *E. farinosa*, it is quite possible that increased leaf pubescence is a relatively simple adaptation that allows a species to occupy habitats of increased aridity, while retaining physiological characteristics suited to more mesic habitats.

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